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Management to control citrus greening alters the soil food web and severity of a pest–disease complex

R. Campos-Herrera [a,b,*], F.E. El-Borai [a,c], T.E. Ebert [a], A. Schumann [a], L.W. Duncan [a]

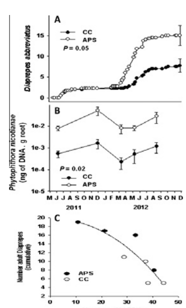
[a] Citrus Research and Education Center (CREC), University of Florida (UF), 700 Experiment Station Road, FL 33850, USA
[b] Instituto de Ciencias Agrarias, CSIC, Serrano 115 Dpdo, Madrid 28006, Spain
[c] Plant Protection Department, Faculty of Agriculture, Zagazig University, Egypt

HIGHLIGHTS

- Advanced production system (APS) speeds citrus tree growth and maturity.
- APS increased abundance of herbivorous arthropods, nematodes and oomycetes.
- APS reduced numbers of steinernematid entomopathogenic nematodes.
- Modification of APS to mitigate these non-target effects may be feasible.

GRAPHICAL ABSTRACT

An advanced production systems (APS) was designed to grow citrus trees more quickly than conventional citriculture (CC) methods to mitigate the impact of the bacterial disease of citrus huanglongbing. Changes in the soil physico-chemical properties caused by daily fertigation in APS increased the abundance of the root herbivore *Diaprepes abbreviatus* (A) and the root rotting oomycete *Phytophthora nicotianae* (B). APS had additional non-target effects on some species of native entomopathogenic nematodes (EPNs; C) reported to modulate population growth of both *D. abbreviatus* and *P. nicotianae*.



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ABSTRACT

Since 2005, the Florida citrus industry has faced the need to control the devasting bacterial disease huanglongbing (HLB). Advanced production systems (APS) were designed to grow citrus trees more quickly than conventional citriculture (CC) methods in order to mitigate the impact of HLB. Daily fertigation required by APS produces changes in the soil physical–chemical properties compared to those in conventionally managed orchards. We used real-time PCR in an ongoing field experiment to compare the effects of APS and CC on more than a dozen metazoan and microorganism species in soil food webs that affect larvae of a major arthropod pest of citrus, *Diaprepes abbreviatus*. Soil chemical properties, citrus performance, weevil occurrence, and abundance of free-living and plant-parasitic nematodes were also evaluated. The effects of polypropylene mulch that provides a barrier to soil entry by *D. abbreviatus* larvae were also investigated in each of the two cultural systems. Trees grew significantly larger in APS and mulching increased tree growth and reduced tree mortality, thereby increasing fruit yield per ha. APS increased the fruit yield in 2011; however, by 2013 the number of fruit per tree was not affected by any of the treatments. Root mass density increased in APS, but decreased under mulch. The numbers of plant-parasitic and free-living nematodes and some natural enemies of nematodes such as *Catenaria* sp. and *Paecilomyces lilacinus* were more abundant in the treatments with greater root mass density. Both organisms in the *D. abbreviatus*–*Phytophthora nicotianae* pest–disease complex were more abundant in

* Corresponding author at: Citrus Research and Education Center (CREC), University of Florida (UF), 700 Experiment Station Road, FL 33850, USA. Fax: +1 863 956 4631.
E-mail addresses: r.camposherrera@ufl.edu, raquel.campos@ica.csic.es (R. Campos-Herrera).

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APS than in CC, whereas fewer steinernematid entomopathogenic nematodes (EPNs) that prey on insect larvae occurred in APS. By contrast, heterorhabditid EPNs tended to be more numerous in APS than in CC, although they comprised <25% of the EPN communities in any treatment. Major differences between APS and CC in almost all of the measured physical and chemical soil properties provide a basis for controlled studies to understand why EPN taxa responded differently to these treatments and how APS and soils generally might be modified to conserve the beneficial activities of nematodes.

1. Introduction

Entomopathogenic nematodes (EPNs) belonging to the families Heterorhabditidae and Steinernematidae are obligate pathogens of soilborne arthropods (Georgis et al., 2006). These nematodes are virtually ubiquitous in soils of all continents except Antarctica (Adams et al., 2006). In Florida, native entomopathogenic nematodes (EPNs) are important natural enemies of the key citrus pest *Diaprepes abbreviatus* (Dolinski et al., 2012). The larvae of this weevil reside exclusively in the soil where, during several months of development, they cause extensive damage to the fibrous and woody roots of citrus trees and facilitate infection by the phytopathogenic oomycetes *Phytophthora nicotianae* and *Phytophthora palmivora* (Graham et al., 2003). Naturally occurring EPNs killed weevil larvae buried in orchards at rate exceeding 50% per week and variability in the regional abundance of weevils may be linked to the species diversity and community composition of native EPN species (Duncan et al., 2003, 2007, 2013; Futch et al., 2005; Campos-Herrera et al., 2013a).

Advanced production system (APS) is a term applied to an 'open hydroponic' method of citriculture in which trees are fertigated daily via drip or microsprinkler irrigation systems. The new system is being studied as a method to bring young trees to maturity more rapidly to recoup the investment in an orchard as quickly as possible, before trees become non-productive due to the bacterial disease huanglongbing (citrus greening) (Schumann et al., 2013). First detected in Florida in 2005, the bacterial pathogen and its psyllid vector are ubiquitous in the citrus growing regions where they threaten the existence of the industry (Graham et al., 2013). If widely adopted, APS will fundamentally change the physical/chemical properties of orchard soil, compared to soil under conventional citriculture (CC) where trees are irrigated only periodically and fertilized just 3–4 times per year. These changes could alter soil food webs in ways that affect the health of the trees. For example, APS was detrimental to native *Steinernema diaprepesi* and exotic *Steinernema riobrave* applied to soil (Campos-Herrera et al. 2013b). However, augmented *Heterorhabditis indica* persisted equally well in APS and CC plots. The bacterium *Paenibacillus* sp., a species-specific phoretic associate of *S. diaprepesi* that impairs nematode motility (El-Borai et al., 2005; Enright and Griffin, 2005), was more abundant on the cuticles of *S. diaprepesi* in APS plots (Campos-Herrera et al., 2013b). These bacteria may have contributed to reducing *S. diaprepesi* in APS, whereas molecular monitoring of several species of nematophagous fungi recovered from the nematode samples did not implicate any of the fungal natural enemies as potentially affecting the EPNs differently in the two citriculture systems (Campos-Herrera et al., 2013b).

S. diaprepesi was more effective than other native EPN species at protecting citrus seedlings from *D. abbreviatus* in long-term greenhouse trials (El-Borai et al., 2007, 2012). The nematode is commonly encountered on Florida's central ridge eco-region where weevil abundance is typically low, but not in coastal flatwoods eco-regions where *D. abbreviatus* are most abundant (Campos-Herrera et al., 2013a). Understanding the edaphic factors that affect the abundance of *S. diaprepesi* might reveal ways in which soil can be modified to enhance and conserve the biocontrol potential of the nematode. Because APS is detrimental to steinernematids (Campos-Herrera et al., 2013b), we conducted studies in the ongoing trial of Schumann et al. (2013) to determine whether non-target effects of the two citriculture systems (APS and CC) on EPNs can affect biological control of *D. abbreviatus*, citrus health and fruit yield. In addition, we installed and evaluated the biotic and abiotic effects of landscape fabric mulch that enhances citrus growth and prevents weevil infestation of the soil beneath the tree canopy (McKenzie et al., 2001; Duncan et al., 2009). We hypothesized that (i) APS would continue to decrease the numbers of *S. diaprepesi* and, thereby, increase the numbers of *D. abbreviatus* emerging from the soil and *Phytophthora* sp. infecting roots and (ii) fabric mulch would decrease numbers of *D. abbreviatus*, thereby, increasing root mass density, tree size and fruit yield in both APS and CC.

2. Materials and methods

2.1. Field experiment design and treatments

The study were conducted in an ongoing experiment located in the central ridge eco-region (Auburndale, Florida, USA, 81:48:44.65 W, 28:06:53.98 N, 49 m elevation above sea level). Four factorial treatments were established to compare the effects of two different horticultural systems and the use of fabric mulch on both citrus growth and the soil food web. Treatments included: (i) the horticultural management systems conventional citriculture (CC) or advanced production system (APS) and (ii) the application of landscape fabric (LSF) or not (bare soil, BS) as a mulch on the soil surface. The horticultural systems were established in spring 2008, each one replicated four times in plots containing four rows (3 m in row $\times$ 6 m between rows) of 35–40 trees (Hamlin orange on Swingle citrumelo rootstock) in a randomized complete block design. Details of the managements, crop history, map representation and establishment were described by Schumann et al. (2012, 2013) and Campos-Herrera et al. (2013b). Each plot ($n = 4$) was divided into 3 subareas, in each of which soil beneath 3 adjacent trees was covered with landscape fabric (Lumite 994GC, woven polyester landscaping fabric, Synthetic Industries, Gainesville, GA) in September 2009. Two pieces of fabric (1.8 m $\times$ 9 m long) were stretched over the soil surface on each side of the three trees and secured with steel staples pounded into the soil. Slits cut into the fabric allowed each piece to overlap the other by 30 cm at the tree line while tightly surrounding the tree trunks. The final dimensions of the mulch were 3 m wide by 9 m long. Three tree plots immediately adjacent to the mulched trees were selected for the bare soil comparison. At each sampling time, the abiotic and biotic variables measured in each of the three subareas were averaged (e.g., $n = 4$ plots per treatment).

2.2. Sampling methods and chemical analysis

Soil in each subarea was sampled five times during two years: July 27th 2011, December 7th 2011, March 27th 2012, May 29th 2012 and August 21st 2012. On each date, the steel staples were